

A review of Australian fossil penguins (Aves: Sphenisciformes)

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Abstract

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Australian fossil penguins (Sphenisciformes) are reviewed as a basis for future primary research. The five named species are based on type specimens of Eocene, Miocene—Pliocene and Holocene age collected from South Australia, Victoria and Tasmania. The phylogenetic affinities of these taxa remain unresolved. Only one type specimen is represented by clearly associated elements of a skeleton; the rest are single bones (isolated partial humeri and a pelvis). Further research is required to establish the taxonomic status of *Pachydyptes simpsoni*, *Anthropodyptes gilli*, *Pseudaptenodytes macraei*, *?Pseudaptenodytes minor* and *Tasidyptes hunteri*. Additional described specimens include isolated postcranial elements from the Late Oligocene of South Australia and Late Miocene—Early Pliocene of Victoria. Other Miocene and Pliocene specimens are housed in Museum Victoria. These specimens have the potential to shed light on the Neogene palaeobiogeography and diversification of crown group penguins.

Keywords

South Australia, Tasmania, Victoria, Cenozoic, evolution, bird

Introduction

The published fossil record of penguins (Sphenisciformes) in Australia, although limited compared to that of Antarctica, New Zealand and South America, spans some 40 million years from the late Eocene to Recent (Ksepka and Ando, 2011). The majority of previous work has been produced by one author (Simpson, 1957, 1959, 1965, 1970) with the last primary research conducted by Van Tets and O'Connor (1983). Since then, several summaries have been published (Jenkins, 1985; Fordyce & Jones, 1990; Vickers-Rich, 1991). Current work underway by the authors indicates that many undescribed diagnostic specimens reside in museum collections. The aim of this work is to introduce the Sphenisciformes, summarise current knowledge of Australian fossil penguins, discuss implications for penguin evolution, and outline both gaps in knowledge and opportunities for future research.

Definitions and Terminology

This review follows the traditional classification of penguins where Sphenisciformes is the Order to which the single family, Spheniscidae, belongs. Spheniscidae contains all known species of penguin, fossil and extant. The terms Sphenisciformes and Spheniscidae are therefore used interchangeably throughout this paper. Osteological terminology and terms of orientation follows that of Baumel and Witmer (1993).

Institutional Abbreviations

ANWC, Australian National Wildlife Collection, CSIRO Division of Wildlife and Rangelands Research, Canberra, Australia; NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia; SAM P, South Australian Museum Palaeontology Collection, Adelaide, Australia.

The Sphenisciformes

Sphenisciformes (penguins) are a group of flightless marine birds confined to the southern hemisphere. Contrary to popular stereotype, not all species reside in Antarctica, with the highest species diversity found in New Zealand (Ksepka et al., 2012) and one species (the Galapagos penguin, *Spheniscus mendiculus* Sundevall, 1871 actually living at the equator (Vargas et al., 2005; Jadwiszczak, 2009). Fossil species are found in the same regions as extant species (Simpson, 1975), with Antarctica, Australia, New Zealand, South Africa, and South America all possessing both fossil and extant assemblages. Present regional species diversities roughly correspond to past levels, with areas such as New Zealand and Antarctica well represented by numerous fossil and living species, despite the fossil record not being continuous throughout the Cenozoic (Ksepka & Ando, 2011; Ksepka et al., 2012) (Fig. 1). One of the most specialised avian groups (Kaiser, 2007), the morphology of living penguins is well known (Pycraft, 1898; Lowe, 1933; Marples, 1952) and they have evolved a range of adaptations to an aquatic lifestyle including: small and scale-

like feathers; increased underwater visual acuity (Sivak & Millodot, 1977; Bowmaker & Martin, 1985); several retia mirabilia systems for efficient thermoregulation (Frost et al., 1975; Thomas & Fordyce, 2007, 2012); stiffening of wing joints (Raikow et al., 1998); relative shortening of the wing; hydrodynamic flattening of wing elements; and shortening of the tarsometatarsus. The Sphenisciformes differ from most avian groups in that total diversity was greater in the past than present, with 19 extant species (sensu Ksepka & Ando, 2011), and 53 recognised fossil species (Fig. 2). This is testament to their aquatic lifestyle and the fact that particular penguin bones (e.g. humerus, tarsometatarsus) are more likely to fossilise than their equivalents in other avian groups due to their pachyostotic histology (Meister, 1962). Extant species feed on small fish, cephalopods, crustaceans and plankton, and show little interspecific postcranial morphological variation (Olson, 1985). Interspecific differences in cranial morphology are minimal; the differences that do occur probably reflect disparate feeding ecology (Zusi, 1975).

Origin of Sphenisciformes

The fossil record of penguins is one of the longest and relatively complete of any of the neornithine groups, potentially allowing scientists to test hypotheses regarding the physical drivers of vertebrate evolution e.g. climate change, palaeoceanography (Baker et al., 2006; Ksepka & Thomas, 2012), biogeography (Clarke et al., 2007), secondary adaptation to water (Thomas & Fordyce, 2007), and stratigraphic calibration of molecular divergence estimates (Slack et al., 2006). Thus the penguin fossil record informs broader issues in macroevolution.

The oldest known penguin, *Waimanu manneringi* Jones, Ando and Fordyce, 2006, is from the early Paleocene (60.5 – 61.6 Ma) of New Zealand (Slack et al., 2006). Although archaic, it is clearly a penguin and already flightless. Simpson (1946) summarised previous theories of penguin evolution (e.g. Lowe, 1933) and concluded that penguins evolved directly from a volant ancestor, with no intermediate terrestrial stage. Molecular data estimate the divergence of Sphenisciformes from their sister taxon, Procellariiformes, about 71 Ma during the Cretaceous (Baker et al., 2006; Brown et al., 2008). Slack et al., (2006) wrote that the origins of Sphenisciformes took place 90–100 Ma as part of the Late Cretaceous neornithine radiation. It has been proposed that once the loss of aerial flight had occurred the adaptation of penguins to an aquatic lifestyle occurred rapidly due to the opening of ecological niches left by the extinction of most marine reptiles at the end of the Cretaceous and the intensive selection pressures of entering a new “adaptive zone” (Fordyce & Jones, 1990).

Some fossil species reached giant sizes (e.g. *Anthropornis nordenskjöldi* Wiman, 1905, *Pachydyptes ponderosus* Oliver, 1930) of 1.5 – 1.6 m in standing height (Jadwiszczak, 2001), far exceeding that of today's largest species *Aptenodytes forsteri* Gray, 1844 (emperor penguin), which rarely exceeds 1.0 m (Friedmann, 1945; Stonehouse, 1975; Ksepka et al., 2012). Nonetheless, estimated heights of giant taxa may be overestimates following the first discovery of body proportions in a nearly complete stem penguin (Ksepka et al., 2012). These giant species (and potentially all stem species) are thought to have fed on fish,

using their slender bills to spear large prey (Olson, 1985; Myrcha et al., 1990, 2002; Ksepka et al., 2008). This contrasts with extant species, which tend to have shorter beaks (*Aptenodytes* is an exception) and feed on smaller fish (Zusi, 1975). This trophic specialisation is thought to have occurred relatively late in penguin evolution (Ksepka & Bertelli, 2006), with elongate, narrow beaks representing the ancestral condition (Clarke et al., 2007). Fossil feathers are known from *Inkayacu paracasensis* Clarke et al., 2010, a species from the Eocene of Peru. These show not only that the key features of penguin wing feathers had evolved early in penguin evolution, but that this particular species was reddish-brown and grey, considerably different from the iconic black and white colouration of extant penguins (Clarke et al., 2010).

Considerable effort over the last two decades has been aimed at resolving penguin phylogeny including extinct taxa (Sibley & Ahlquist, 1990; Baker et al., 2006; Gianni & Bertelli, 2004; Bertelli & Gianni, 2005; Bertelli et al., 2006; Ksepka et al., 2006; Slack et al., 2006; Walsh & Suarez, 2006; Clarke et al., 2007; Acosta Hospitaleche et al., 2007, 2008). There is a general consensus between morphological and molecular data (Fig. 2), apart from the issues of where the phylogenies are rooted (Livezey, 1989), and the timing of the divergence of the crown Spheniscidae (Clarke et al., 2007). Basal penguins form a paraphyletic group, with higher morphological disparity compared to crown Spheniscidae (Davis and Renner, 2003). This is most likely due to the relatively recent common ancestry and broadly similar feeding ecology of the crown Spheniscidae (Zusi, 1975). The timing of the crown clade's divergence from stem Sphenisciformes is still unresolved, as molecular and morphological data give different estimates of ca. 41 Ma (Middle Eocene) and 11–13 Ma (Middle-Late Miocene), respectively (Baker et al., 2006; Göhlich, 2007). All pre-Miocene taxa are stem Sphenisciformes (Ksepka & Clarke, 2010), rendering the fossil record incongruent with the ancient divergence estimated from molecular data.

Australian fossil Sphenisciformes

The record of Sphenisciformes in Australia is less extensive than that of New Zealand, South America and Antarctica, with a chronologically scattered distribution and the majority of fossils being fragmentary. This limited record probably reflects a lack of systematic field exploration, collecting and research, rather than real rarity of fossils. Until now, the majority of fossil penguin discoveries have been fortuitous in nature. Despite this relatively meagre record, penguins are known from ten localities limited to southeast Australia in every geologic epoch from the Eocene onwards (Figs. 1 and 3; Table 1).

Eocene. Six specimens in total have been described from this epoch (Finlayson, 1938; Glaessner, 1955; Simpson, 1957; Jenkins, 1974), including the partial skeleton (SAM P14157) of an indeterminate form resembling the Antarctic genus *Anthropornis* (Jenkins, 1974; Jenkins, 1985) (Fig. 4; Table 2). Found at Blanche Point, South Australia and originally named as *Pachydyptes simpsoni*, it is the most complete fossil penguin yet discovered in Australia. Other specimens referred to this *Anthropornis*-like form include a partial right humerus (SAM P14158a) (Fig. 5;

Table 1. Summary of Australian fossil penguin localities. Abbreviations: E, east; NNW, north northwest; S, south; SSW, south southwest;

Locality	Geographic Location	Coordinates	Age (Ma)	Stratigraphic position	Reference(s)
Blanche Point	37 km SSW of Adelaide, South Australia.	35°14'S, 138°27'E	Late Eocene (36.5–38.0)	Blanche Point Formation	Alley et al., 1995; Jenkins et al., 1982; James and Bone, 2000
Witton Bluff	South end of Christie's Beach, about 26 km SSW of Adelaide, South Australia.	35°09'S, 138°28'E	Late Eocene (36.5–38.0)	“	“
Mount Gambier	Pritchard Brothers' building stone quarry, about 11 km west of Mount Gambier, South Australia.	37°49'S, 140°38'E	Early–Late Oligocene (23.0–30.0)	Gambier Limestone	Alley et al., 1995; Li et al., 2000; Fitzgerald, 2004
Devil's Den	On east bank of Glenelg River, about 17 km NNW of Dartmoor, Victoria. Site is marked “Bw” on the map published by Singleton (1941, p. 46).	37°46'S, 141°14'E	Early Miocene (17.6–21.0)	Gellibrand Marl	Gill, 1959a; Jenkins, 1974; Abele et al., 1988; Dickinson et al., 2002
Batesford Quarry	Australian Cement Company quarry south of Batesford, on the western bank of the Moorabool River, west of Geelong.	38°06'S, 144°17'E	Early–Middle Miocene (15.9–17.6)	Batesford Limestone	Abele et al., 1988; Gourley and Gallagher, 2004
			Middle Miocene (13.7–15.9)	Fyansford Formation	Abele et al., 1988; Gourley and Gallagher, 2004
Portland	Beach on western side of Portland Bay, at Portland, Victoria.	38°20'S, 141°36'E	Late Miocene (6.0–9.8)	Port Campbell Limestone	Mallett, 1977; Abele et al., 1988; Dickinson et al., 2002
Spring Creek	Northeast of Minhamite, 41 km southeast of Hamilton, Victoria.	37°58'S, 142°23'E	Late Miocene–Early Pliocene (5.0–6.0)	Goodwood Formation	Gill, 1964; Simpson, 1970; Abele et al., 1988; Holdgate and Gallagher, 2003
Beaumaris	East of Rickett's Point on west shore of Beaumaris Bay, on northeast shore of Port Phillip Bay.	37°59'S, 145°03'E	Late Miocene–Early Pliocene (5.0–6.2)	Black Rock Sandstone	Abele et al., 1988; Dickinson and Wallace, 2009
Red Bluff	About 3.5 km southwest of Lake Tyers, east of Lakes Entrance, East Gippsland, Victoria.	37°52'S, 148°03'E	Late Pliocene (2.5–3.5)	Jemmy's Point Formation	Abele et al., 1988; Wallace et al., 2005
Amphitheatre Cave	Approximately 6 km north of Nelson, south-western Victoria.	38°03'S, 141°01'E	Holocene	Cave pitfall assemblage	Baird, 1992
Hunter Island	Stockyard Site, Hunter Island, 5 km north of Tasmania.	40°32'S, 144°45'E	Holocene	Aboriginal midden	Van Tets and O'Connor, 1983

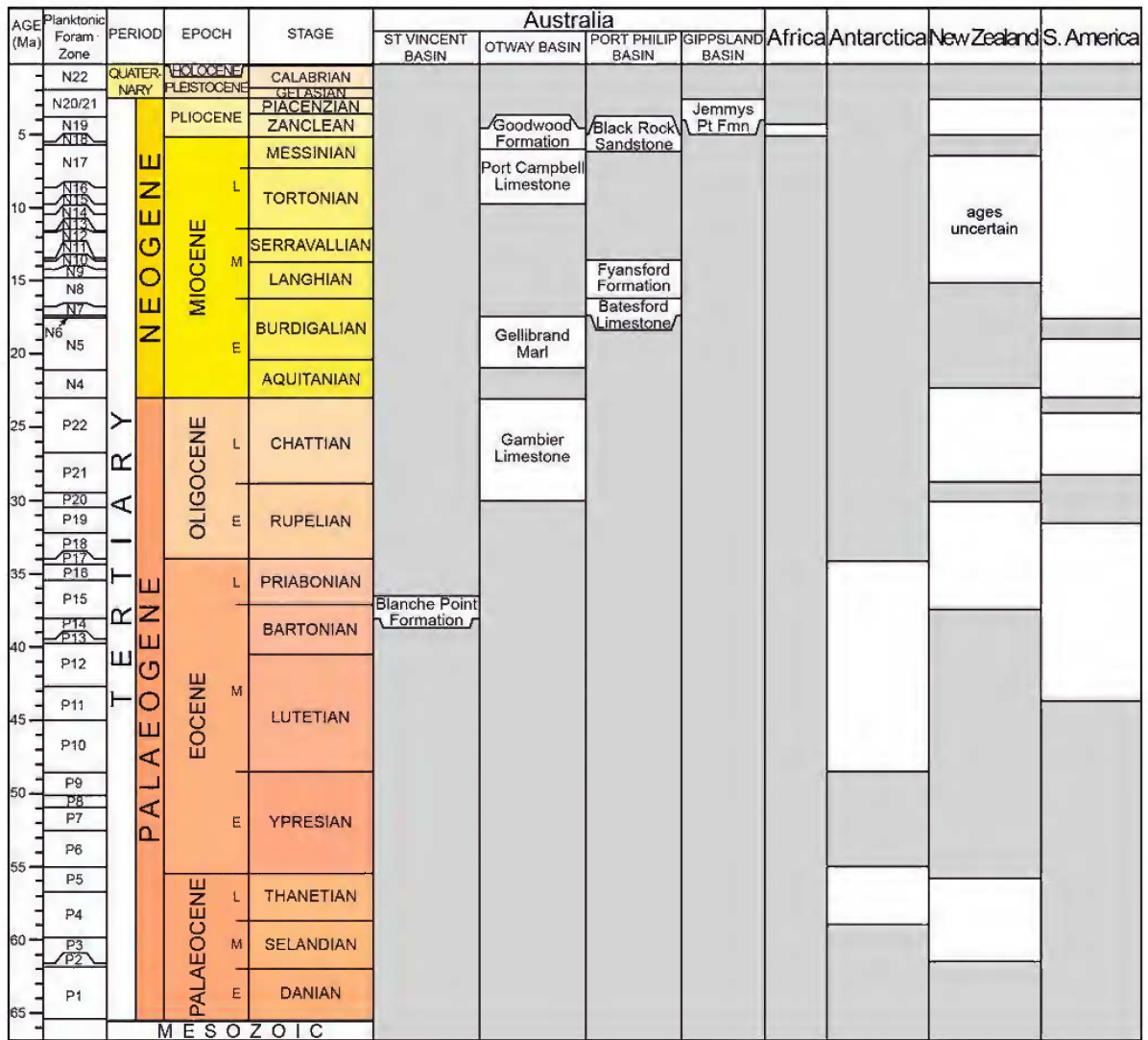


Figure 1. Chronostratigraphy and correlation of Australian fossil penguin-bearing units, compared with the fossil record of Sphenisciformes on other continents. Note that the vertical ranges of stratigraphic units represent estimates of geologic age maxima and minima for penguin-bearing horizons, not necessarily discrete time-spans of deposition. Geologic timescale is after Gradstein et al. (2004) with updates from Walker and Geissman (2009). See Table 1 for references to ages of Australian units. Ages of African units: Hendey (1981); Roberts et al. (2011); Ksepka and Thomas (2012). Ages of Antarctic units: Dingle and Lavelle (2000); Jadwiszczak (2006); Marensi et al. (2012). Ages of New Zealand units: White and Waterhouse (1993); Cooper (2004); Slack et al. (2006); Ksepka et al. (2012). Ages of South American units: Devries (1998); Scasso et al. (2001); Celma and Cantalamessa (2007); Achurra et al. (2009); Malumián and Nájuez (2011); Uhen et al. (2011).

Table 2), a partial right radius (SAM P14158b) (Fig. 5; Table 2), and a partial rib (SAM P17913; Table 2). A second form originally thought to be closely related to *Palaeodyptes* was described by Finlayson (1938), who reported a left humerus (SAM P7158) (Fig. 6; Table 2) from Witton Bluff, South Australia. A right tibiotarsus (SAM P10862) (Fig. 7; Table 2), also from Witton Bluff was noted by Glaessner (1955), described by Simpson (1957), and also referred to this form. Simpson (1971)

subsequently reassigned this material to Sphenisciformes, indeterminate. A third form, intermediate in size between the *Palaeodyptes* and *Anthropornis* forms is known from two bones, one allegedly found at Blanche Point and the other from late Eocene rocks near Browns Creek, Otway Peninsula, Victoria (Jenkins, 1985; Vickers-Rich, 1991). These two specimens have not been described, and recent efforts by one of us (EMGF) to locate them in the SAM and MV collections have failed.

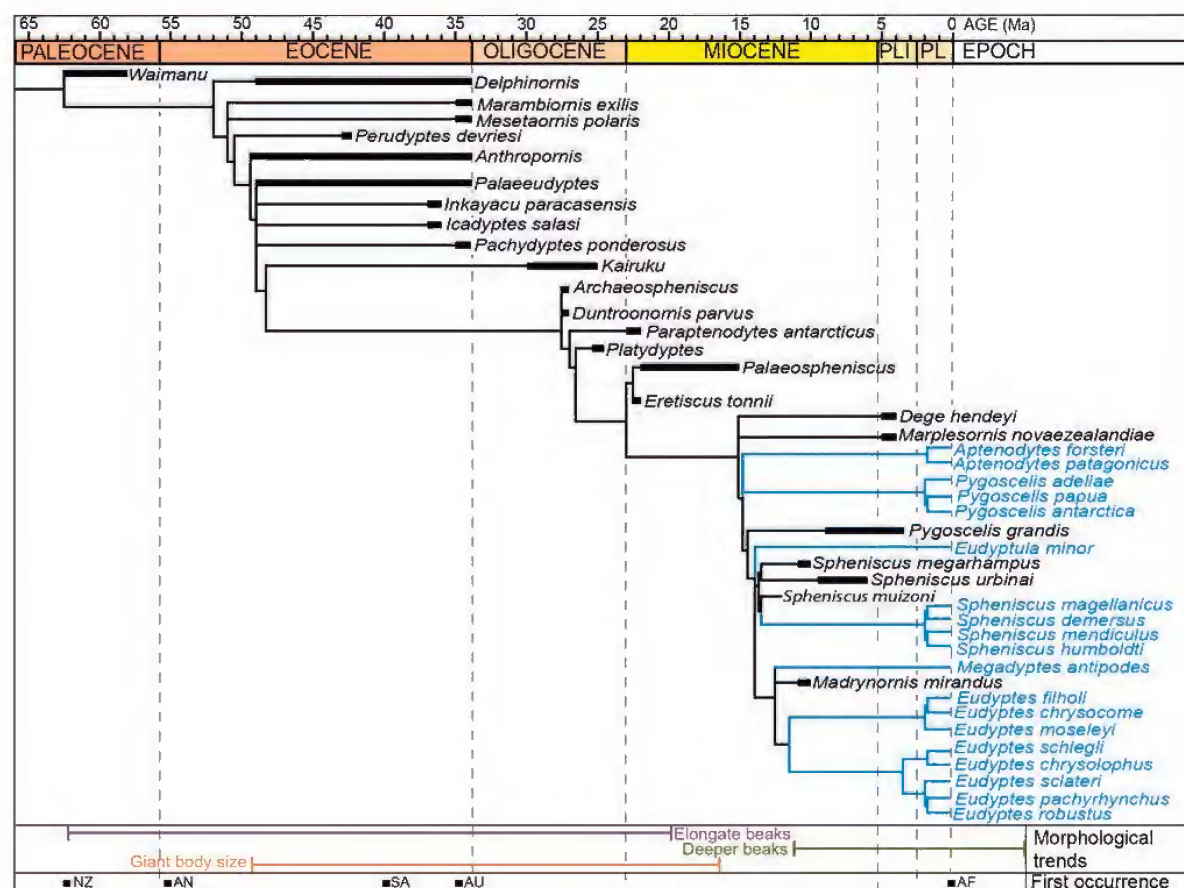


Figure 2. Temporally-calibrated phylogeny of Sphenisciformes modified from Ksepka and Ando (2011) and Ksepka et al. (2012), showing major trends in Sphenisciform evolution and the first occurrence of Sphenisciformes in each region with extant species. Stem sphenisciform branches are shown in black and crown clade Spheniscidae branches are shown in blue. Thick horizontal bars on branches indicate stratigraphic range maxima and minima. Abbreviations: AF, Africa; AN, Antarctica; AU, Australia; Ma, million years ago; SA, South America.

Oligocene. Only two fossil penguin specimens are known from the Oligocene of Australia. Both of them were derived from the Camelback Member of the Gambier Limestone, which has been correlated to the P21/22 planktonic foram zone (Lower–Upper Oligocene) (Li et al., 2000). Both specimens, a partial right humerus (SAM P10863) (Fig. 8; Table 2) and a partial left femur (SAM P10870) (Fig. 9; Table 2), were first noted by Glaessner (1955) and later described by Simpson (1957). Neither of the specimens has been assigned to a genus or species, but they are considered to be separate taxa (Simpson, 1957).

Early–Middle Miocene. Fossil penguin specimens have been described from the Early–Late Miocene of Australia. A single specimen was found as float on the banks of the Glenelg River at Devil's Den, Victoria (Gill, 1959a; Simpson, 1959). The large right humerus (NMV P17167) was named as *Anthropodyptes gilli* by Simpson (1959) (Fig. 10; Table 2). From the Early Miocene (Gill, 1959a; Jenkins, 1974; Dickinson et al., 2002), it is

the latest surviving giant stem Spheniscid known, although some extinct crown Spheniscid taxa (e.g. *Spheniscus megaramphus*) would have been larger than *Aptenodytes forsteri* (Ksepka & Clarke, 2010; Stucchi, 2003). As yet undescribed material has also been collected from the Lower–Middle Miocene Batesford Limestone at Batesford, near Geelong, Victoria including: a partial right femur (NMV P222904), a partial left femur (NMV P201867), and a partial left coracoid (NMV P231933). A partial left tibiotarsus (NMV P231836) and a partial right femur (NMV P201856) have also been collected from the Middle Miocene Fyansford Clay at the same locality.

Late Miocene–Pliocene. Mio–Pliocene penguins have been described from two localities: Spring Creek, near Minnamite, and Beaumaris, Victoria. Simpson (1965, 1970), described a total of 21 penguin specimens from these localities. From Spring Creek an incomplete left humerus (NMV P26668, holotype of *Pseudaptenodytes macraei* Simpson, 1970) (Fig. 11; Table 2),

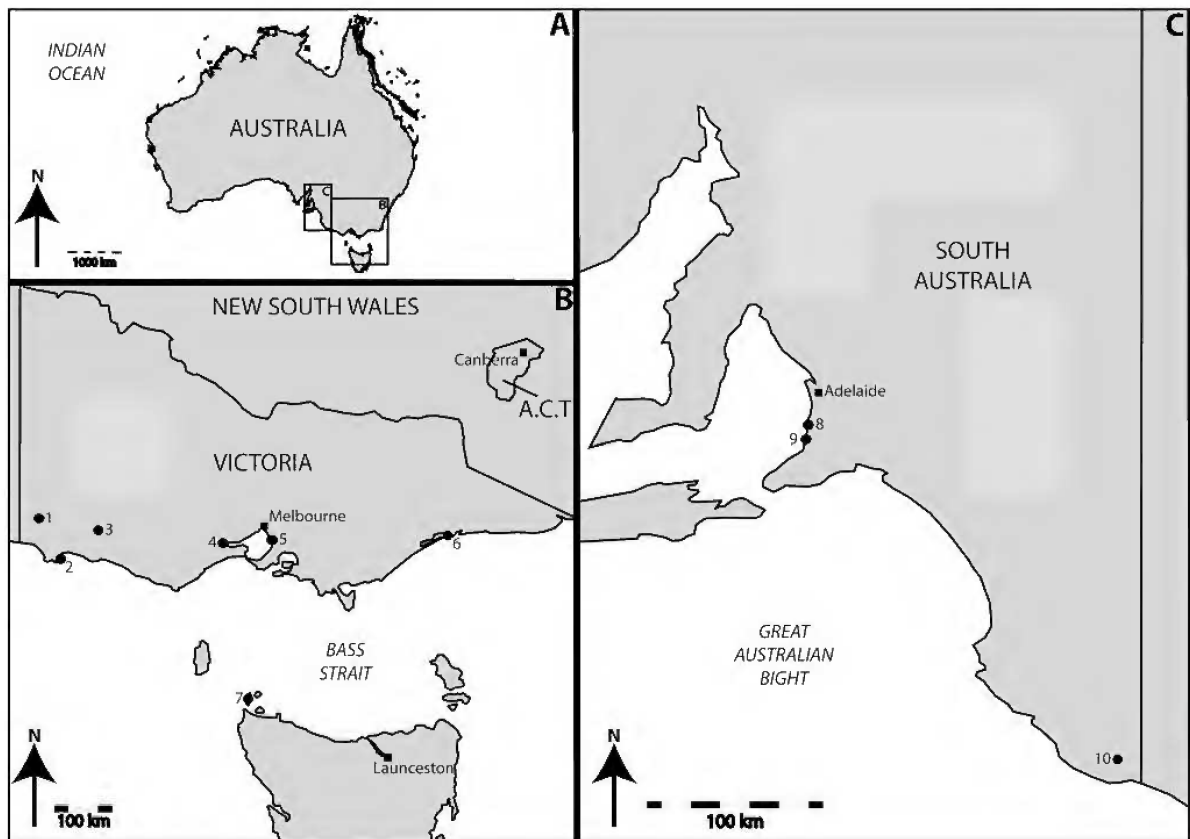


Figure 3. Fossil sphenisciform localities in Australia. 1 = Devil's Den; 2 = Portland; 3 = Spring Creek; 4 = Batesford Quarry; 5 = Beaumaris; 6 = Red Bluff; 7 = Hunter Island; 8 = Witten Bluff; 9 = Blanche Point; 10 = Mount Gambier

and from Beaumaris: a partial left coracoid (NMV P24065) (Simpson, 1965) (Fig. 12; Table 2); three partial left humeri (NMV P26671, NMV P26676, NMV P27059) (Fig. 13; Table 2); four partial right humeri (NMV P26669, NMV P26677, NMV P27057, NMV P26670) including the holotype of *?Pseudaptenodytes minor* Simpson, 1970 (NMV P26669) (Figs. 13 and 14; Table 2); four partial carpometacarpi (NMV P27055, NMV P27056, NMV P27058, NMV P26903) (Figs. 13 and 15; Table 2); and eight isolated fragments (registration numbers unspecified by Simpson, 1970). The *P. macraei* humerus is the larger of the two species, being similar in size to the humerus of a king penguin (*Aptenodytes patagonicus* Miller, 1778), whereas the *?P. minor* humerus approaches that of the gentoo penguin (*Pygoscelis papua* Forster, 1781) in size. *?Pseudaptenodytes minor* was referred to Sphenisciformes indet. by Ksepka and Ando (2011: 159). The Upper Miocene Port Campbell Limestone at Portland, Victoria, has yielded a nearly complete left humerus (NMV P221273) and a partial left humerus (NMV P232062). One definitively Pliocene specimen is known from Australia, an undescribed partial right femur (NMV P41738) from the

Pliocene Jemmys Point Formation at Red Bluff, west of Lake Tyers, Victoria.

Holocene. Van Tets and O'Connor (1983) described penguin remains from a ca. 760 year-old aboriginal midden on Hunter Island, Tasmania and described these as a new genus and species, *Tasidyptes hunteri*. Other workers (Fordyce and Jones, 1990; Ksepka and Clarke, 2010) have doubted this identification due to the fragmentary nature of the fossils: the coracoid (ANWC BS2669) (Table 2) and tarsometatarsus (ANWC BS2668) (Table 2) are indistinguishable from *Eudyptes*; and the four specimens comprising the hypodigm (ANWC BS2667, ANWC BS2668, ANWC BS2669, ANWC BS2670) (Table 2) come from three different horizons within the midden (Van Tets and O'Connor, 1983; Fordyce and Jones 1990; Ksepka and Clarke, 2010). Baird (1992) reported little penguin (*Eudyptula minor* Forster 1781) material from a pitfall assemblage in Amphitheatre Cave, Victoria which has been dated to ca. 4670 ybp (Table 2). However, this *Eudyptula* material is unlikely to be from the original pitfall assemblage due its differential preservation (Baird, 1992: 31–32).

Table 2. Described fossil penguin specimens from Australia. Abbreviations: ANWC, Australian National Wildlife Collection; indet., indeterminate; Ma, million years ago; NMV P, Museum Victoria Palaeontology Collection; SA, South Australia; SAM P, South Australian Museum Palaeontology Collection; TAS, Tasmania; VIC, Victoria.

Specimen	Taxon (previous assignment)	Material	Locality (Formation)	Age (Ma)	Reference(s)
SAM P7158	Sphenisciformes indet. (cf. <i>Palaeudyptes</i>)	left humerus	Witton Bluff, SA (Blanche Point Formation, Tuketja Member)	Late Eocene (36.5–38.0)	Finlayson, 1938; Simpson, 1957
SAM P10862	“	right tibiotarsus	Witton Bluff, SA (Blanche Point Formation, Gull Rock Member)	“	Glaessner, 1955; Simpson, 1957
SAM P14157 (a–g)	Sphenisciformes indet. (<i>Pachydyptes simpsoni</i>)	partial skeleton	Blanche Point, SA (Blanche Point Formation, Gull Rock Member)	“	Jenkins, 1974
SAM P14158a	“	partial right humerus	Blanche Point, SA (Blanche Point Formation, Tuketja Member)	“	“
SAM P14158b	“	partial right radius	“	“	“
SAM P17913	“	partial rib	“	“	“
SAM P10863	Sphenisciformes indet.	partial right humerus	Mt. Gambier, SA (Gambier Limestone)	Early–Late Oligocene (~23.0–30.0)	Glaessner, 1955; Simpson, 1957
SAM P10870	“	partial left femur	Mt. Gambier, SA (Gambier Limestone)	Early–Late Oligocene (~23.0–30.0)	Simpson, 1957
NMV P17167	<i>Anthropodyptes gilli</i>	right humerus	Glenelg River, Devil’s Den, VIC (Gellibrand Marl)	Early Miocene (17.6–21.0)	Simpson, 1959; Gill, 1959a
NMV P24065	Sphenisciformes indet.	partial left coracoid	Beaumaris, VIC (Black Rock Sandstone)	Late Miocene–Early Pliocene (5.0–6.0)	Simpson, 1965
NMV P26668	<i>Pseudaptenodytes macraei</i>	partial left humerus	Spring Creek, Minhamite, VIC (Goodwood Formation)	Late Miocene–Early Pliocene (5.0–6.0)	Gill, 1964; Simpson, 1970
NMV P27055	cf. <i>Pseudaptenodytes macraei</i>	partial right carpometacarpus	Beaumaris, VIC (Black Rock Sandstone)	Late Miocene–Early Pliocene (5.0–6.0)	Simpson, 1970
NMV P27056	cf. <i>Pseudaptenodytes macraei</i>	partial left carpometacarpus	“	“	“
NMV P26669	Sphenisciformes indet. (? <i>Pseudaptenodytes minor</i>)	partial right humerus	“	“	“
NMV P26677	“	“	“	“	“
NMV P26670	“	“	“	“	“
NMV P27057	“	“	“	“	“
NMV P26671	“	partial left humerus	“	“	“
NMV P26676	“	“	“	“	“
NMV P27058	“	partial right carpometacarpus	“	“	“
NMV P26903	“	right carpometacarpus	“	“	“
NMV P27059	Sphenisciformes indet.	partial left humerus	“	“	“
N/A	“	isolated fragments (8)	“	“	“
ANWC BS2667	Sphenisciformes indet. (<i>Tasidyptes hunteri</i>)	juvenile synsacrum	Hunter Island, TAS (Aboriginal midden)	Holocene (ca. 760 ybp)	Van Tets and O’Connor, 1983
ANWC BS2668	<i>Eudyptes</i> sp. (<i>Tasidyptes hunteri</i>)	left tarsometatarsus	“	“	“
ANWC BS2669	“	left coracoid	“	“	“
ANWC BS2670	Sphenisciformes indet. (<i>Tasidyptes hunteri</i>)	pelvis	“	“	“
NMV P178677	<i>Eudyptula minor</i>	proximal pelvis	Amphitheatre Cave, VIC (pitfall assemblage)	Holocene (ca. 760 ybp)	Baird, 1992
NMV P178678	<i>Eudyptula minor</i>	right femur	“	“	“
NMV P178679	<i>Eudyptula minor</i>	left femur	“	“	“
NMV P178680	<i>Eudyptula minor</i>	partial left tibiotarsus	“	“	“
NMV P178681	<i>Eudyptula minor</i>	partial left tarsometatarsus	“	“	“

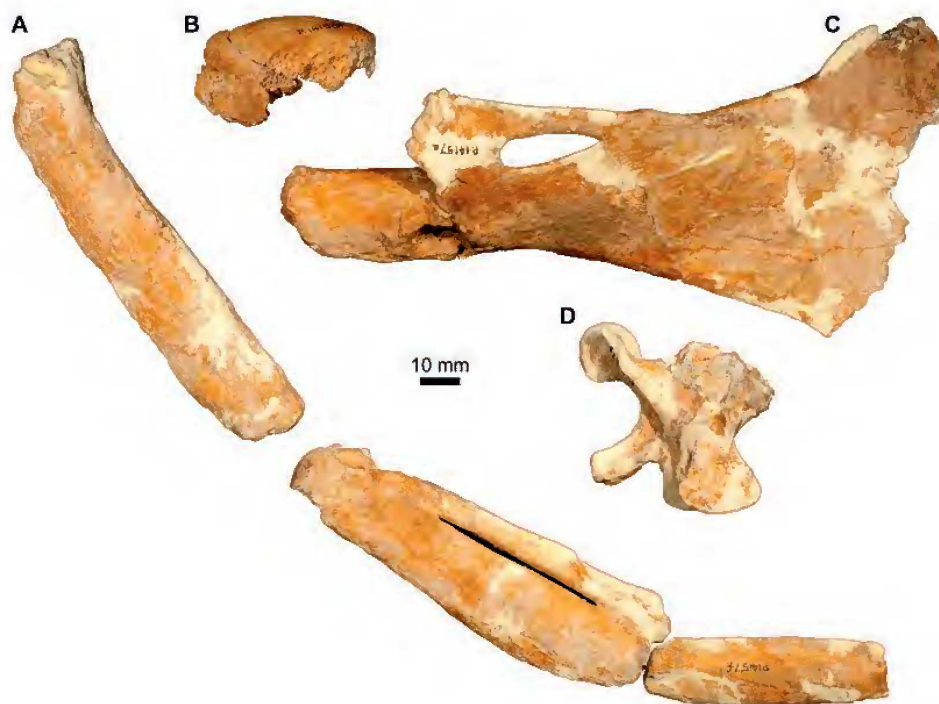


Figure 4. *Pachydyptes simpsoni* holotype, SAM P14157: A, right radius in ventral view, left carpometacarpus and left phalanx II-1 in dorsal view; B, head of right humerus in dorsal view; C, left coracoid in dorsal view; D, ?twelfth cervical vertebra in ventral view.

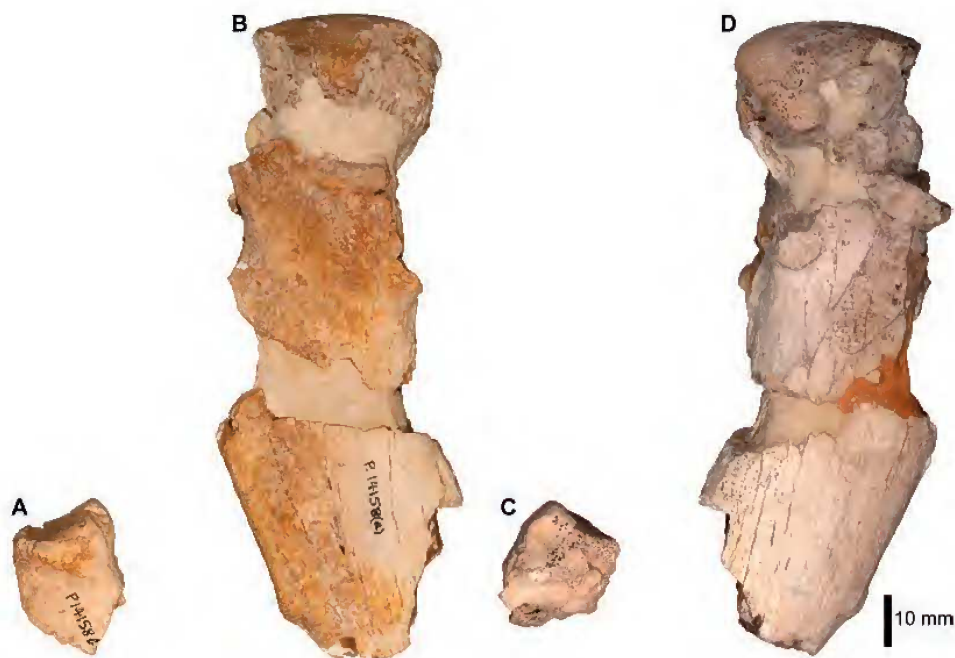


Figure 5. *Pachydyptes simpsoni* paratype, SAM P14158: proximal end of right radius in (A) ventral view and (C) dorsal view; partial right humerus in (B) ventral and (D) dorsal views.

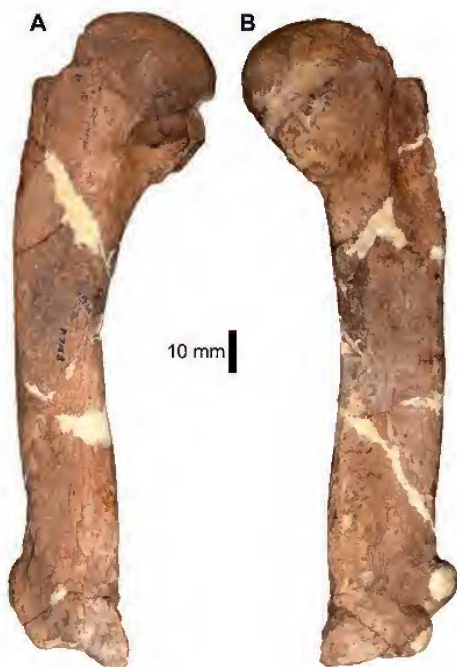


Figure 6. *Sphenisciformes* indet. left humerus, SAM P7158: A, dorsal view; B, ventral view.



Figure 7. *Sphenisciformes* indet. partial right tibiotarsus, SAM P10862: A, cranial view; B, caudal view.

Systematic Palaeontology

A total of five species of fossil penguin have been named from Australia. Only one taxon is based on a type specimen consisting of associated remains. The remaining four species are established on isolated elements. Only two of these five species are currently considered taxonomically distinct (*Anthropodyptes gilli* and *Pseudaptenodytes macraei*).

Aves Linnaeus, 1758

Sphenisciformes Sharpe, 1891

Spheniscidae Bonaparte, 1831

Pachydyptes Oliver, 1930

Pachydyptes simpsoni Jenkins, 1974

Holotype. Partial skeleton (SAM P14157) consisting of: a partial left coracoid; partial right humerus; partial left humerus; a right radius; a partial left carpometacarpus; a left phalanx II-1; and a partial vertebra. (Fig. 4; Table 2).

Type locality. Blanche Point, 37 km SSW of Adelaide, South Australia (35°14'S, 138°27'E).

Horizon and age. Occurs in the Gull Rock Member and the Tuketja Member of the Blanche Point Formation. The Gull

Rock Member consists of green and grey, glauconitic and fossiliferous calcareous mudstone with a few limestone lenses; the Tuketja Member consists of alternating bands of tough, dark grey chert and friable clays, silts and calcareous clays (Jenkins et al., 1982). Both members are in the P15 foraminiferal zone; Late Eocene (Bartonian–Priabonian), 36.5–38.0 Ma (James and Bone, 2000).

Referred material. A partial right humerus (SAM P14158a) (Fig. 5), a partial right radius (SAM P14158b) (Fig. 5) and a rib fragment (SAM P17913). (Table 2)

Diagnosis. Following Marples (1952), the generic diagnosis of *Pachydyptes* is as follows : humerus relatively wide; m. deltoideus minor insertion (referred to as the 'external tuberosity' by Marples, 1952) projects distally; articular surface flattened; fossa pneumotricipitalis undivided; m. supracoracoideus insertion slightly oblique, almost parallel to long axis of shaft and widely separated from the m. latissimus dorsi insertion; shaft has slight sigmoid curve and slight angulation of the cranial border; angle between long axis of shaft and tangent of condylus dorsalis and condylus ventralis is acute; shelf adjacent to condylus ventralis approximately the same width as condylus ventralis; and coracoid convex at base. Following Jenkins (1974), *Pachydyptes simpsoni* differs from *Pachydyptes ponderosus* Oliver, 1930 by having: more concave medial margin of the coracoid; more pronounced angulation of the cranial margin of the humerus (referred to as the "preaxial



Figure 8. Sphenisciformes indet. partial right humerus, SAM P10863: A, dorsal view; B, ventral view.

tuberosity on the shaft at the proximal limit of attachment of brachialis internus” by Jenkins, 1974); more widely separated insertions of the musculus supracoracoideus and the musculus coracobrachialis caudalis (referred to as the pectoralis secundus and pectoralis tertius respectively by Jenkins, 1974); metacarpal III extends further distally than metacarpal II; and the bones are generally less robust.

Remarks. The referred humerus (SAM P14158a) is similar to *Pachydyptes ponderosus* with its large head, expanded muscle attachments and wide shaft. The skeleton however is overall less robust than *P. ponderosus* and the overall morphology of the coracoid, radius and carpometacarpus shows similarities to *Anthropornis* and *Palaeodyptes* (Jenkins, 1974). The coracoid has a broadly flared base and an oval foramen nervi supracoracoidei. On the radius, the insertion site of the m. brachialis is hollowed, forming a distinct notch similar to that of *Paraptenodyptes robustus* Ameghino, 1905, although the bone itself resembles that of *Palaeodyptes* and *Anthropornis* (Jenkins, 1974). Systematic revisions of *Pachydyptes simpsoni* have seen it first synonymised with *Anthropornis nordenskjöldi* (Jenkins, 1985), and most recently considered as *Sphenisciformes* indet. (Ksepka and Clarke, 2010). The latter authors concluded that it occupied a more crownward position than Antarctic *A. nordenskjöldi* specimens. We therefore consider the systematics of *P. simpsoni* to be unresolved.



Figure 9. Sphenisciformes indet. partial left femur, SAM P10870: A, dorsal view; B, ventral view.

Anthropodyptes Simpson, 1959

Anthropodyptes gilli Simpson, 1959

Holotype. Right humerus (NMV P17167). (Fig. 10; Table 2).

Type locality. Specimen was found as float on top of Miocene marl on east bank of Glenelg River at Devil's Den, about 17 km NNW of Dartmoor, Victoria. Site is marked “Bw” on the map published by Singleton (1941: 46) (37°46'S, 141°14'E).

Horizon and age. Gill (1959a) determined that NMV P17167 was derived from the Gellibrand Marl, which at this locality represents planktonic foraminiferal zones N5–N6, Early Miocene (Aquitainian–Burdigalian), 17.6–21.0 Ma (Jenkins, 1974: 292; Abele et al., 1988:285; Dickinson et al., 2002).

Diagnosis. Simpson (1957: 118) notes that *Anthropodyptes* does not share any diagnostic characters with any previously named genus. Generic characteristics as follows: humerus slender and elongate; shaft slightly sigmoid, with moderate angulation of the cranial margin; the proximal part of the shaft is narrower than the distal part; fossa pneumaticipitalis undivided and large proximo-distally; m. supracoracoideus insertion wide and slightly oblique, almost parallel to long axis of the shaft; angle between long axis of shaft and tangent of condylus dorsalis and condylus ventralis is about 42°; the condylus ventralis is only slightly ventral to the condylus dorsalis; shelf adjacent to condylus ventralis smaller than condylus ventralis.



Figure 10. *Anthropodyptes gilli* holotype right humerus, NMV P17167: A, dorsal view; B, ventral view.

Remarks. This species is apparently most similar to *Archaeospheniscus* (Gill, 1959b; Simpson, 1959: 118), a Late Oligocene New Zealand form. Based on synapomorphies, *Anthropodyptes gilli* has a most exclusive placement of clade 8 in the phylogenetic analysis of Ksepka and Clarke (2010: Fig. 21), giving it a more crown-ward position than earlier 'giant' forms from the late Eocene, but a similar phylogenetic position to late Oligocene giant forms such as *Kairuku* and *Archaeospheniscus*. *Anthropodyptes gilli* bears the distinction of being the latest surviving giant stem penguin, all other 'giant' stem taxa having a Palaeogene age (Ksepka and Clarke, 2010: 45). Comparisons of body proportions with other giant taxa are not possible until more complete material is found.

Pseudapterodyptes Simpson, 1970

Pseudapterodyptes macraei Simpson, 1970

Holotype. Partial left humerus (NMV P26668). (Fig. 11; Table 2).

Type locality. Spring Creek near Minhamite, 41 km southeast of Hamilton, Victoria (37°58'S, 142°23'E).

Horizon and age. The holotype is derived from the Goodwood Formation, a green-grey marly fine sand with abundant pebbles (Gill, 1964:332). The macroinvertebrate assemblage is similar to that of the Upper Miocene–Lower Pliocene Black



Figure 11. *Pseudapterodyptes macraei* holotype left humerus, NMV P26668: A, dorsal view; B, dorso-caudal view; C, ventral view.

Rock Sandstone (Gill, 1964; Simpson, 1970), and the Goodwood Formation is possibly laterally equivalent to the Upper Miocene–Lower Pliocene Grange Burn Formation (Fitzgerald, 2004).

Referred material. A partial right carpometacarpus (NMV P27055) and a partial left carpometacarpus (NMV P27056) were tentatively referred to this species (Simpson, 1970) (Fig. 15; Table 2). Both specimens were derived from the Upper Miocene–Lower Pliocene Black Rock Sandstone at Beaumaris.

Diagnosis. Simpson (1970) noted the very close similarity of *Pseudapterodyptes macraei* to *Aptenodytes patagonicus*, both in terms of size and the features of the proximal end of the humerus. Nevertheless, *P. macraei* differs from *Aptenodytes* by having a humerus with: a more sigmoid shaft; a smaller volume of the fossa pneumotricipitalis; a distinctly oval opening of the internal division of the fossa pneumotricipitalis; and a rounded cranial margin lacking a distinct 'preaxial angle' (Acosta Hospitaleche et al., 2008: Fig. 5, char. 11). It further differs from *A. forsteri* by lacking the pit for ligament insertion on the proximal surface adjacent to the head (Ksepka et al., 2006: Fig. 8). In *A. patagonicus* this feature is variable (Ksepka et al., 2006).

Remarks. Despite the similarities of the type specimen to *Aptenodytes patagonicus*, *Pseudapterodyptes macraei* is not ancestral to it or any of the modern species (Simpson, 1970:



Figure 12. Sphenisciformes indet. partial left coracoid, NMV P24065: A, dorsal view; B, ventral view.

20). Although similar, the autapomorphies of NMV P26668 preclude this specimen from referral to *Aptenodytes* or any extant genera. We consider *P. macraei* to be a distinct taxon established on the basis of a diagnostic type specimen.

?*Pseudaptenodytes minor* Simpson, 1970

Holotype. Partial right humerus (NMV P26669). (Fig. 14; Table 2).

Type locality. East of Rickett's Point on the western shore of Beaumaris Bay, northeast shore of Port Phillip Bay, Victoria (37°59'S, 145°03'E).

Horizon and age. Black Rock Sandstone, which consists of a basal layer of phosphatic and ferruginous intraclasts overlain by calcareous sandstone (Dickinson and Wallace, 2009). Planktonic foram and molluscan biostratigraphy indicate a Late Miocene–Early Pliocene age range, which is corroborated by Sr dates of 5.0–6.2 Ma (Dickinson and Wallace, 2009).

Referred material. Distal end of right humerus (NMV P26677), proximal end of left humerus, (NMV P26671), proximal end of left humerus (NMV P26676), right humerus (NMV P26670), right humerus (NMV P27057), partial right carpometacarpus (NMV P27058), right carpometacarpus (NMV P26903) (Fig. 13; Table 2). All referred material was collected from the Upper Miocene–Lower Pliocene Black Rock Sandstone at Beaumaris.

Diagnosis. Differs from *Pseudaptenodytes macraei* by having: a more slender and less sigmoid shaft; and a less expanded distal section (Simpson, 1970). It also differs by having a distinct angle on the cranial margin, although this angulation is still less than that of any modern penguin (Simpson, 1970).

Remarks. Simpson (1970) notes the similarities between ?*Pseudaptenodytes minor* and *Paraptenodytes robustus* yet the holotype of ?*P. minor* is too incomplete to permit meaningful comparisons. The lack of diagnostic morphology in the type specimen of ?*P. minor* has resulted in Ksepka and Clarke (2010) referring this taxon to Sphenisciformes indet. More completely preserved material is required to confirm or reject the placement of this species in *Pseudaptenodytes*. The additional material referred by Simpson (1970) to ?*P. minor* displays little overlap in morphology with the holotype (NMV P26669). Furthermore, it is only on the basis of the referred material that the holotype was designated a species of *Pseudaptenodytes*. We therefore recommend restricting the concept of ?*P. minor* to the holotype. All referred material should be considered Sphenisciformes indet. pending further study.

***Tasidyptes* Van Tets and O'Connor, 1983**

***Tasidyptes hunteri* Van Tets and O'Connor, 1983**

Holotype. Pelvis in three parts (ANWC BS2670) (Table 2).

Type locality. Stockyard Site, Hunter Island, 5 km north of Tasmania (40°32'S, 144°45'E).

Horizon and age. Material found in an aboriginal midden. Carbon dating resulted in an age of 760 ± 70 ybp (Holocene).

Referred material. The paratype specimen is a left tarsometatarsus (ANWC BS2668). Also referred to the species are a juvenile synsacrum (ANWC BS2667) and a left coracoid (ANWC BS2669). (Table 2)

Diagnosis. Differs from *Eudyptula* and *Megadyptes* by having: a caudal part of the synsacrum with relatively broader fused vertebrae and long slender lateral processes; and the lateral foramen vasculare proximale situated more distal than the medial foramen vasculare proximale on the plantar surface of the tarsometatarsus. However, this character is not clear from the figure in Van Tets and O'Connor (1983: Fig. 4).

Remarks. This taxon is no longer considered valid due to the fragmentary nature of the fossils, the fact that the coracoid and tarsometatarsus are indistinguishable from *Eudyptes* and the fact that the four specimens come from three different stratigraphic layers of the midden (Van Tets and O'Connor, 1983; Fordyce and Jones, 1990; Ksepka and Clarke, 2010). However, Ksepka and Clarke (2010) note that due to the young age of the specimens, DNA testing to confirm their identity may well be possible. Ksepka and Ando (2011: 178) also draw attention to the synsacrum stating that the long slender lateral processes may be "a possible diagnostic character, certainly in need of quantitative evaluation".

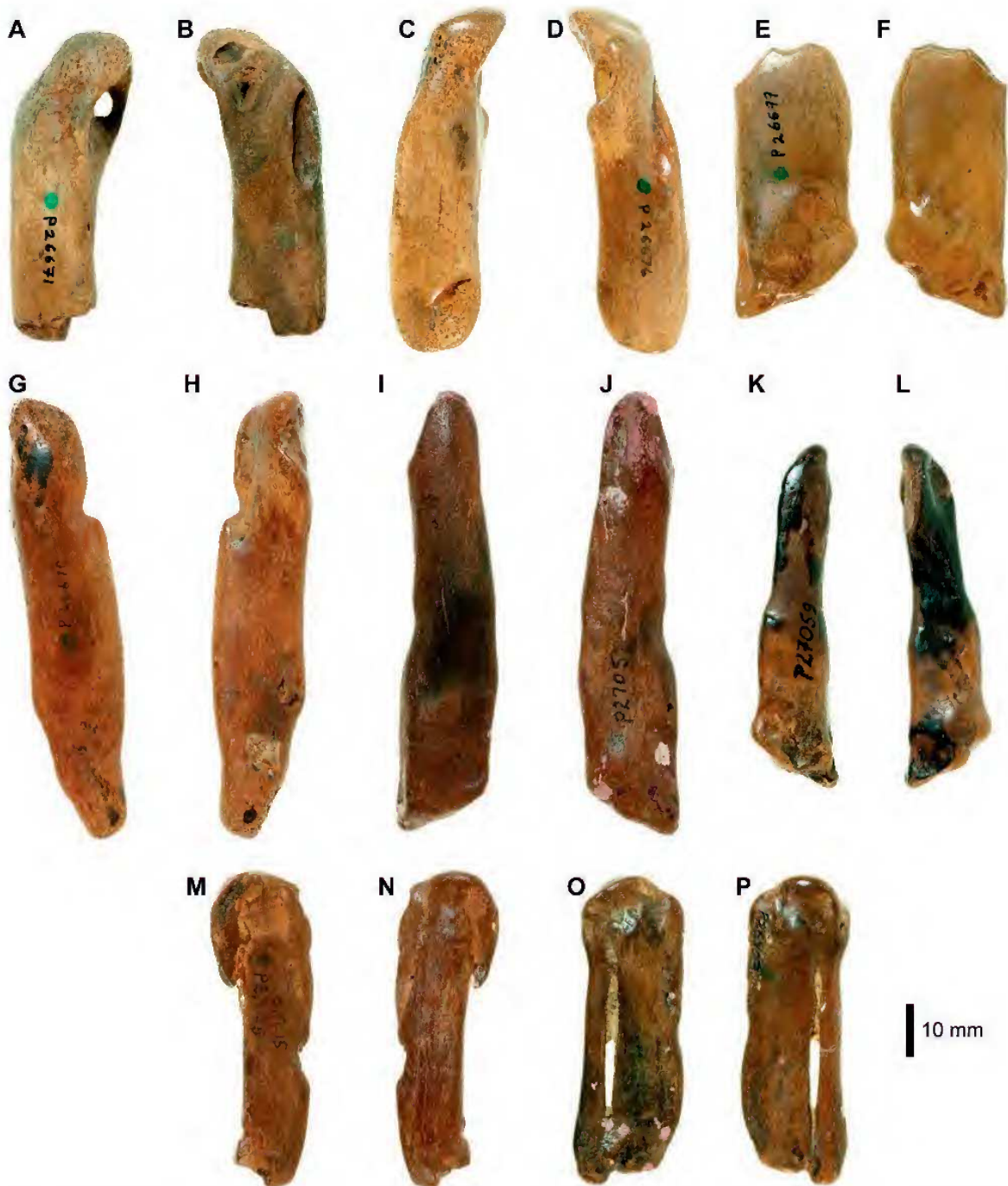


Figure 13. Sphenisciformes from the Upper Miocene–Lower Pliocene Black Rock Sandstone, Victoria. A–J and M–P, specimens referred to *?Pseudaptendytes minor*: partial left humerus, NMV P 26671, in (A) dorsal and (B) ventral views; partial left humerus, NMV P26676, in (C) dorsal and (D) ventral views; partial right humerus, NMV P26677, in (E) dorsal and (F) ventral views; partial right humerus, NMV P26670, in (G) dorsal and (H) ventral views; partial right humerus, NMV P27057, in (I) dorsal and (J) ventral views; partial right carpometacarpus, NMV P27058, in (M) dorsal and (N) ventral views; partial right carpometacarpus, NMV P26903, in (O) dorsal and (P) ventral views. Sphenisciformes indet. partial left humerus, NMV P27059: K, dorsal view; L, ventral view.



Figure 14. *Pseudaptenodytes minor* holotype partial right humerus, NMV P26669: A, dorsal view; B, ventral view.

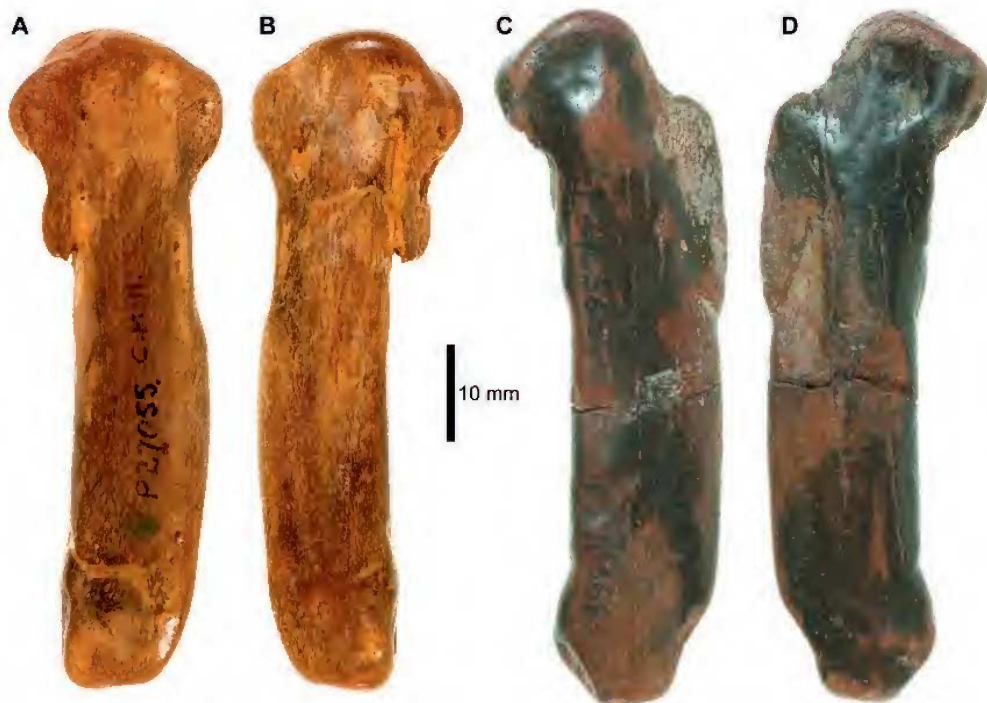


Figure 15. Specimens referred to *Pseudaptenodytes macraei*: partial right carpometacarpus, NMV P27055, in (A) dorsal and (B) ventral views; partial left carpometacarpus, NMV P27056, in (C) ventral and (D) dorsal views.

Discussion

The Australian penguin record has thus far played a minor role in the interpretation of sphenisciform evolutionary history. Despite there being general summaries (Jenkins, 1985; Fordyce and Jones, 1990; Vickers-Rich, 1991), no primary systematic research has been conducted since 1983.

With this limited quantity of described material, what patterns may be deduced from the fossil record of penguins in Australia? As shown above, the record has a scattered chronologic distribution and is based on fragmentary fossils. Nonetheless, the vast majority of all fossil penguin specimens ever found are isolated and often incomplete elements (see Acosta Hospitaleche et al., 2007; Ksepka et al., 2008, 2012 for exceptions). Second, there is a disparity between past and present taxonomic diversity. During the Eocene, Oligocene and Miocene there were more than one species of penguin inhabiting Australia. All these species were larger than the sole extant species, *Eudyptula minor* Forster, 1781 (little penguin), although body sizes have yet to be estimated using established regression equations (e.g. Simpson, 1946; Jadwiszczak, 2001). This higher taxonomic diversity and morphological disparity relative to the present remains unexplained. A possible causal factor promoting higher diversity is the former increased availability of suitable breeding grounds due to higher sea levels forming numerous small offshore islands. An example of this is known from the Pliocene of Africa (Ksepka and Thomas, 2012).

The Australian record includes penguin material from the Early through late Miocene. This interval is inadequately sampled worldwide (Ksepka and Ando, 2011: 157–163), and thus Australian fossils may provide insights into this pivotal period in penguin history, including the diversification of crown Spheniscidae.

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